JHR 96: 657–666 (2023)
doi: 10.3897/jhr.96.107379
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

A new compression fossil, *Eotriadomeroides abjunctus* Huber, gen. & sp. nov. (Hymenoptera, Mymaridae), in Eocene shale from the Kishenehn Formation, USA

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Academic editor: Petr Janšta | Received 1 June 2023 | Accepted 31 July 2023 | Published 15 August 2023

https://zoobank.org/D3EF3F05-9185-41B9-A524-1CAC7B9C2D6B

Citation: Huber JT, Greenwalt DE (2023) A new compression fossil, *Eotriadomeroides abjunctus* Huber, gen. & sp. nov. (Hymenoptera, Mymaridae), in Eocene shale from the Kishenehn Formation, USA. Journal of Hymenoptera Research 96: 657–666. https://doi.org/10.3897/jhr.96.107379

Abstract

A new fossil genus and species of fairyfly, *Eotriadomeroides abjunctus* Huber & Greenwalt, **gen.** and **sp. nov.** (Hymenoptera: Chalcidoidea: Mymaridae), is described and illustrated from a female preserved as a compression fossil in middle Eocene shale from the Kishenehn Formation, Montana, USA. It is compared to extant species of *Neotriadomerus* Huber, known only from Australia, and *Triadomerus* Yoshimoto, a Cretaceous amber fossil from Canada. It is suggested that these three genera, classified together in Triadomerini, likely the most ancestral lineage of Mymaridae, are evidence of the Middle or perhaps Late Jurassic origin of the family.

Keywords

Chalcidoidea, Eocene compression fossil, Mymaridae

Introduction

Parasitoid wasps of the family Mymaridae (Hymenoptera), almost all parasitic in eggs of other insects, are common and widespread, occurring on all continents except Antarctica, from 81°49'N (Hazen Camp, Canada) to 54°57'S (Bahía Aguirre, Tierra del Fuego, Argentina). They also occur on most islands, even those farthest

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from continents, e.g., the Hawaiian Islands, St. Helena, and French Polynesia, or those with harsh climates, e.g., Greenland, Iceland, Auckland Islands, Campbell Island and South Georgia; the latter three more than 50°S. Mymaridae are also one of the two best represented families of Chalcidoidea in the fossil record (the other is Baeomorphidae), represented almost entirely by inclusions in amber (Yoshimoto 1975; Poinar and Huber 2011; Engel et al. 2013). Very few Mymaridae are described from compression fossils (Huber and Greenwalt 2011). The fossil records for the family are from the Cretaceous to the Pleistocene, a duration of at least 100 my, though with a large time gap of about 40 my between the Cretaceous and Tertiary fossils records. A compression fossil specimen from the Kishenehn Formation in Montana, USA, representing a new genus and species, is described here.

Methods

Huber and Greenwalt (2011) described the methods of collecting and photographing insect compression fossils from the Kishenehn Formation. The fossil described below was collected in accordance with the United States Forest Service Special Use Permit HUN465. Greenwalt et al. (2015) described the taphonomy of the Kishenehn Formation.

Measurements, in millimeters, were taken from the photographs as accurately as possible and converted into micrometers (μm). Given that the end points of a structure were not always clear, their measurements were rounded to the nearest 5 μm and should be treated as approximate only. Length/width ratios of the antennal segments were calculated from the millimeter measurements, not from the rounded-off micrometer measurements.

Abbreviations used

fu = funicle segment, **mps** = multiporous plate sensilla. The specimen is deposited in:

NMNH Department of Paleobiology, National Museum of Natural History, Washington, DC, USA.

Results

***Eotriadomeroides* Huber, gen. nov.**
https://zoobank.org/3A127582-2F52-40DF-BDA3-ECDB8FBA27A3
Figs 1–8

Type species. *Eotriadomeroides abjunctus* Huber, here designated.

Diagnosis. Female. Antenna with funicle 8-segmented and clava 1-segmented (Figs 2–5); fore wing with venation extending almost to wing apex, with postmarginal

vein as wide as marginal vein or parastigma and ~2.7× as long as parastigma + marginal + stigmal veins (Fig. 7); tarsi 5-segmented (Fig. 8); fore wing microtrichia apparently extending to base of parastigma; hind wing relatively narrow, with acute apex; ovipositor extending ventral to mesosoma almost to level of head and not exserted posterior to apex of gaster (Fig. 1). Other details are apparently the same as for *Neotriadomerus* Huber, morphologically the genus most similar to *Eotriadomeroides*.

Male. Unknown.

Derivation of genus name. From the Greek, *eos*, meaning early + *Triadomerus* (a compound word derived from Greek, *tries*, meaning three, and *meros*, meaning part, referring to the 3-segmented clava) + the suffix *-oides*, meaning like, resembling. *Eotriadomeroides* (gender masculine) is therefore an "early *Triadomerus*-like" genus, referring to its geological age (the Eocene) and morphological similarity to the two other, evidently related genera: *Neotriadomerus* (with all its species extant) and *Triadomerus* (with its single species extinct).

Relationships. Genera of Mymaridae are usually divided formally into subgenera if females of different species within a given genus have either a 1- or 2-segmented clava, or either a 2- or 3-segmented clava, and the other morphological features are essentially identical. So far, no genus is known to have its included species with either a 1-segmented or a 3-segmented clava but none with a 2-segmented clava. Only one genus (*Anaphes* Haliday) possibly has its included species with a 1-, 2-, or 3-segmented clava but so far *Anaphes* species with 3-segmented clava have yet been described and named. Examination of the clava of *Eotriadomeroides* does not suggest it is 2- or 3-segmented but rather that it is clearly 1-segmented, i.e., entire (Fig. 5). For comparison, the species of *Eoanaphes* Huber and *Eoeustochus* Huber from the same formation and apparently with the same quality of preservation, are clearly 3-segmented whereas those of *Gonatocerus* Nees are just as clearly 1-segmented (Huber and Greenwalt 2011). If the clava of *E. abjunctus* were 2- or 3-segmented then it could be classified as a subgenus of *Neotriadomerus*, given that all other features, except relative lengths of postmarginal vein to the rest of the venation, are almost the same in both taxa. *Eotriadomeroides* would then key to *Neotriadomerus* in the key to Cretaceous genera of Mymaridae (Poinar and Huber 2011). Another possibility would be to treat *E. abjunctus* as a subgenus within *Triadomerus* Yoshimoto, described from amber from Cedar Lake, Manitoba (Yoshimoto 1975), which is only about 1000 km away from the type locality (the Kishenehn Basin, Montana) of *E. abjunctus*. According to McAlpine and Martin (1969) the actual source of the Cedar Lake amber is more likely to be upstream, along the Saskatoon River either near Saskatoon, Saskatchewan, or Medicine Hat, Alberta, respectively about 650 km and ~280 km from the type locality of *E. abjunctus* as determined from the present day configuration of the localities (essentially unchanged from 46 my years ago). *Triadomerus* does not have the ovipositor extending anteriorly ventral to the mesosoma and it has a relatively short postmarginal vein compared to length of stigma + marginal + parastigmal veins, so we treat *E. abjunctus* as belonging to a new genus, different from both *Neotriadomerus* and *Triadomerus*, both of which have a 3-segmented female clava and are known, respectively, from seven extant and one extinct species. *Eotriadomeroides* is best classified in Triadomerini (Huber 2017) but exact relationships among the genera still need resolution.

***Eotriadomeroides abjunctus* Huber, sp. nov.**
https://zoobank.org/F0BF8666-43A7-4DFA-A7F9-5ED916490407
Figs 1–8

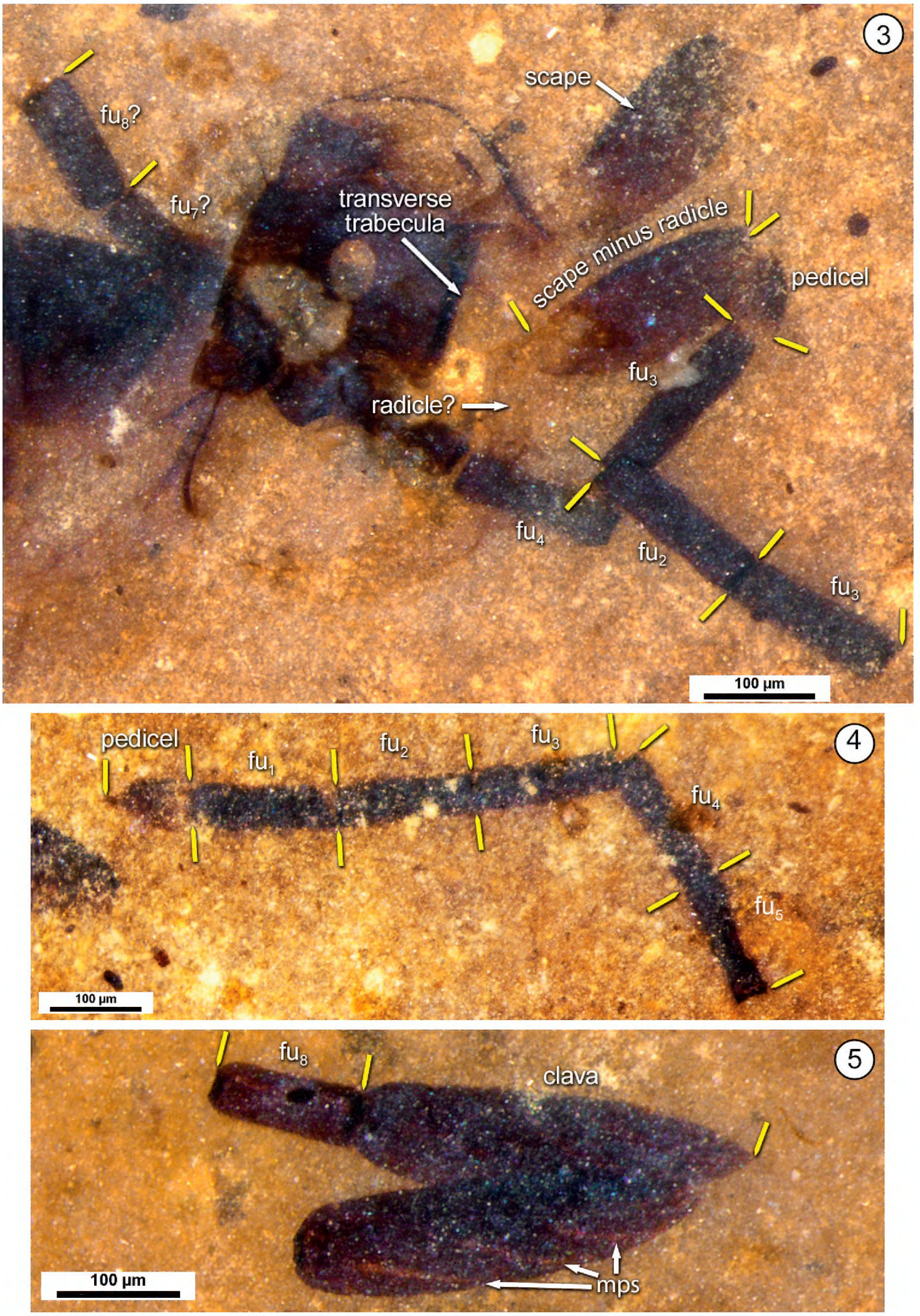
Material examined. ***Holotype*** female (NMNH), on 18 × 14 × 0.15 cm piece of oil shale (Fig. 9), labelled "Holotype *Eotriadomeroides abjunctus* Huber. USNM # PAL 620738". The circle/square scratched onto the surface of the shape indicates the holotype location. The specimen was collected in 2012 at locality #43946, Park site, Kishenehn Formation, Montana, USA.

Diagnosis. *Eotriadomeroides abjunctus* is the only described species in the genus. Its diagnosis is therefore the same as for the generic description. Comparing it with species of morphologically similar genera, it differs from all the described species of *Neotriadomerus* (Huber 2017) as follows: clava 1-segmented (clava 3-segmented in *Neotriadomerus* species); postmarginal vein ~2.7× as long as parastigma + marginal vein + stigmal veins (postmarginal vein at most 0.90× as long in *Neotriadomerus* species); hind wing narrow and apically acute (hind wing wide and apically blunt in *Neotriadomerus* species). The apparent absence of a straight setal line extending from apical margin of fore wing about halfway towards the parastigma + marginal veins (Fig. 7) is an additional feature that may separate *E. abjunctus* from *Neotriadomerus* but the wing surface of *E. abjunctus* is not clear enough to be sure if the setal line is absent. *Eotriadomeroides abjunctus* differs from *Triadomerus bulbosus* Yoshimoto by the clava 1-segmented (3-segmented in *T. bulbosus*), ovipositor extending ventral to mesosoma as far as head (ovipositor not extending anteriorly ventral to mesosoma in *T. bulbosus*), and relatively longer postmarginal vein (relatively shorter in *T. bulbosus*).

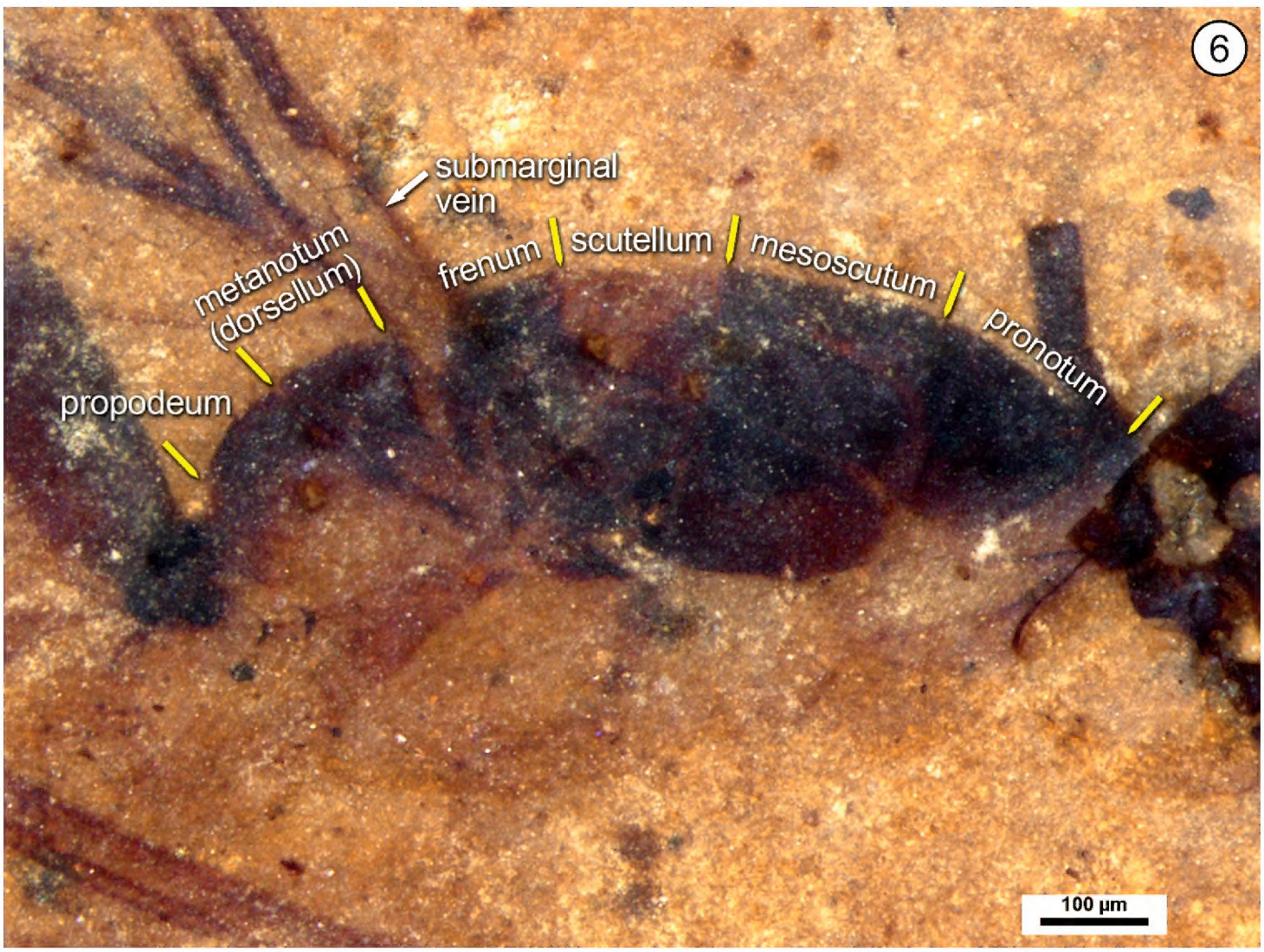
Description. Female. ***Color.*** Vertex, antenna except radicle, dorsum of body, except for scutellum, and ovipositor sheaths dark brown or almost black; face, radicle, scutellum, and mesosoma and metasoma ventrally apparently lighter brown (Fig. 1). ***Total body length*** ~2850. ***Head.*** Head length ~205, head width ~600; mid ocellus diameter ~35. ***Antenna*** (Figs 2–5). Three (possibly 4) mps are visible on the right clava and one on fu_8 of the left antenna (Fig. 5); the mps that most likely should occur on the remaining funicle segments are not visible. Length/width measurements: range (ratios) of antennal segments: radicle? ~85/~12 (2.08), scape excluding radicle ~230/~90 (2.53), pedicel ~75/~50 (1.47), fu_1 ~170/~45 (3.85), fu_2 ~160/~40 (3.83), fu_3 ~150/~40 (3.67), fu_4 ~150/~45 (3.33), fu_5 ~140/~40 (3.08), fu_6 ~150/~40 (3.60), fu_7 ~135/40 (4.00), fu_8 ~125/~150 (2.57), clava ~325/~85 (3.76). ***Mesosoma.*** Mesosoma length ~900, metanotum with dorsellum almost certainly triangular (Fig. 6). ***Wings.*** Fore wing (Fig. 7) with microtrichia uniformly covering entire surface, apparently to base of parastigma and apparently with one row of a few microtrichia posterior to apex of submarginal vein; fore wing length/width ~1930/~560, length/width 3.50, longest marginal setae ~80; hind wing length ~ 1150, width ~45, longest marginal setae ~115, with wing apex acute. ***Legs.*** Tarsi 5-segmented, the tarsomeres becoming shorter towards apex of tarsus (legs segments mostly unrecognizable except two tibiae in part and two tarsi visible, with the end points of basal tarsomeres unclear). ***Metasoma.*** Petiole (Fig. 6) evidently short; gaster with terga apparently about equal in length. Metasoma length ~1875; ovipositor length ~2640, with sheaths extending anteriorly ventral to mesosoma to level of pronotum.

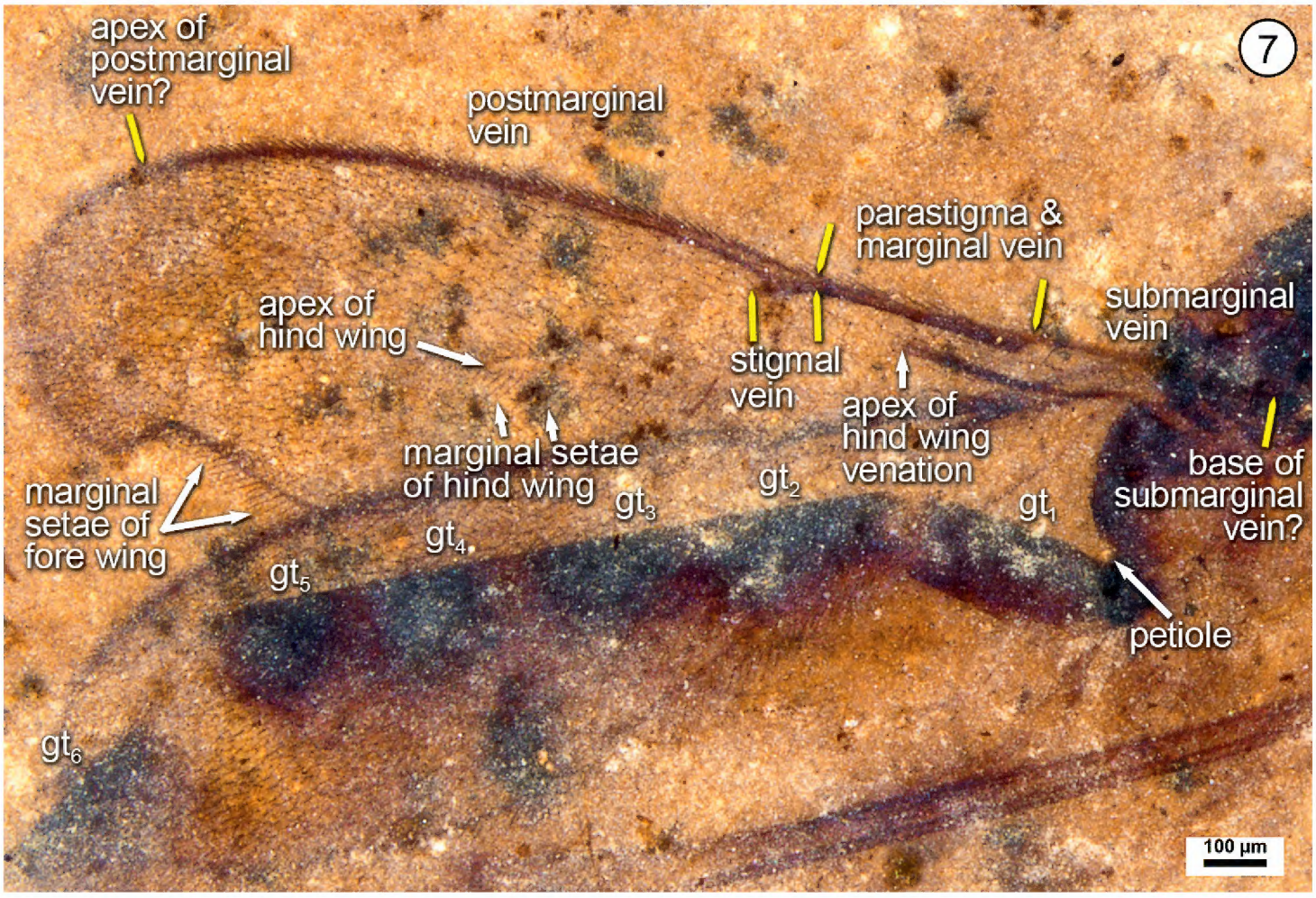
Figures 1, 2. *Eotriadomeroides abjunctus* Huber, holotype female **1** habitus (except most legs not visible) **2** pronotum + head + partly disarticulated antennae.

Derivation of species name. From the Latin *abjunctus*, meaning disunited or separated, refers both to the strongly disjunct geographic distribution of this 40 my old fossil from extant members of *Neotriadomerus*, the most similar looking genus, and to the fact that some of the fossil's appendages are broken into parts (the antennae) or are separated from the body (the legs).

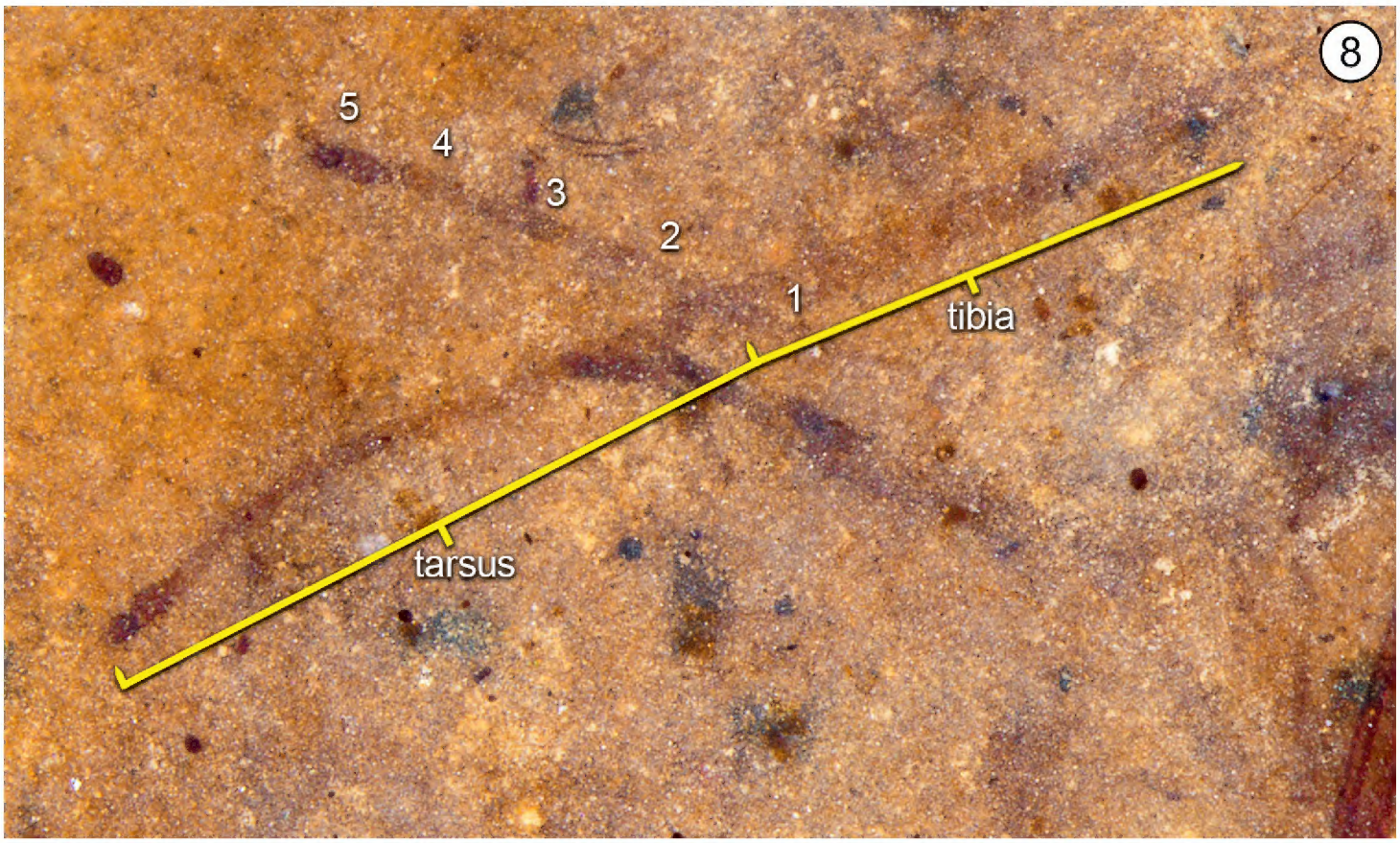


Figures 3–5. *Eotriadomeroides abjunctus* Huber, holotype female **3** head + part of antennae **4** left antenna (pedicel–fu_5) **5** fu_8 + clava of both antennae.





Figures 6, 7. *Eotriadomeroides abjunctus* Huber, holotype female **6** mesosoma **7** wings + metasoma.



Figures 8, 9. *Eotriadomeroides abjunctus* Huber, holotype female **8** tibiae and tarsi of one? pair of legs **9** shale piece containing holotype (circled) of *Eotriadomeroides abjunctus* Huber.

Discussion

Amorim and Greenwalt (2020) described *Synneuron* (Diptera: Canthyloscelidae) from the wings of two fossil specimens, one from the Kishenehn Formation and one from the Koonwarra Fossil Bed in Australia. Given their strongly disjunct (perhaps worldwide) distribution, they suggested the Cretaceous as the minimum age for *Synneuron*, but, more likely, based on their phylogenetic analysis of the tribe it is classified in, they proposed the Middle Jurassic as the minimum age of the genus. *Synneuron* has two extant species, one Palaearctic and the other Nearctic. The case of *Eotriadomeroides* and *Neotriadomerus* may be similar. Although they are classified in different genera, they, together with the Cretaceous genus *Triadomerus*, are best classified in the same lineage, the Triadomerini (Huber 2017), with only the species of *Neotriadomerus* extant. This tribe is likely the most ancestral lineage within Mymaridae, based on its morphology, and its included genera were possibly worldwide in distribution early in the existence of Mymaridae as a recognizable taxon, just as the present day Mymaridae are worldwide. And, as with *Synneuron* and its relatives, the Triadomerini may also have originated as a Pangaean clade. More likely, however, Triadomerini originated more recently, in the middle Jurassic, as estimated by Peters et al. (2018). Regardless of the actual age of origin, Mymaridae are small wasps easily capable of being dispersed aerially for long distances, as evidenced by their current existence on remote islands. So, if they did originate well after the breakup of Pangaea, dispersal worldwide from one or other of those putative centres of origin, either Laurasia or, much more likely, Gondwana would certainly have been possible.

Chronologically, *Eotriadomeroides* (43–46 my), falls almost midway between *Triadomerus* (70–90 my) and *Neotriadomerus* (present day). Evidently, Triadomerini is an ancient lineage that occurs continuously throughout much of the geological history of Mymaridae as currently understood. A related lineage within Triadomerinae, the Aresconini, contains extant species in three genera (Huber 2017), and one extinct species in one genus, *Myanmymar*, from 100 my Burmese amber (Poinar and Huber 2011).One hopes that the large time gaps will eventually be filled as more fossils deposits containing Mymaridae are discovered and better evidence for the age of origin of the family will be found.

The middle Jurassic and early Cretaceous had gymnosperm-dominant environments worldwide, which changed to angiosperm-dominant environments in the later Cretaceous (Wing 2000). This change in flora, presumably accompanied by a similar change in fauna (including perhaps the hosts of Mymaridae), may partly explain why two of the genera (*Eotriadomeroides* and *Triadomerus*) of Triadomerini are extinct and only one genus (*Neotriadomerus*) is extant and found only in the southern Hemisphere, which is where many of the archaic taxa of extant Hymenoptera seem to occur.

The piece of shale that contained *Eotriadomeroides* also contained other synimpressions, as follows: 2 Aphididae and 22 Corixidae (Hemiptera), 16 Chaoboridae, 1 Culicidae and 3 other flies (Diptera), 1 Chalcididae, 1 Chalcidoidea, 1 Formicidae and 1 other wasps (Hymenoptera), 1 Thysanoptera, and 1 plant (Cupressoideae). These insects together suggest they occurred in moist habitat near water.

Acknowledgements

We thank the United States Forest Service for allowing D. Greenwalt to collect compression fossils from the Kishenehn Formation under the auspices of United States Forest Service Special Use Permit HUN465. We gratefully acknowledge the help of Jennifer Read (Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada) for labelling the figures and compiling them into plates.

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